Pinniped Hearing in Complex Acoustic Environments

Dr. Colleen Reichmuth
Institute of Marine Sciences, Long Marine Laboratory
University of California Santa Cruz
100 Shaffer Road
Santa Cruz, CA 95060
phone: (831) 459-3345 fax: (831) 459-3383 email: coll@ucsc.edu

Award Number: N000140610295
http://pinnipedlab.ucsc.edu

LONG-TERM GOALS

Pinnipeds (seals, sea lions, and walruses) are amphibious marine mammals that are susceptible to coastal anthropogenic noise. The long-term goals of this effort are to improve understanding of (1) the sound detection capabilities of several pinniped species, and (2) the effects of noise exposure on the sound detection capabilities of these species. The laboratory and field studies associated with this research will reveal certain aspects of how amphibious mammals receive, perceive, and recognize acoustic information in background noise and will contribute broadly to current knowledge of marine mammal bioacoustics.

OBJECTIVES

Improve understanding of hearing in pinnipeds by extending psychoacoustic profiles of sound reception obtained from simplified auditory processing tasks to those describing performance under increasingly complex acoustic conditions. Relate laboratory measurements to concurrent field studies of communication in fluctuating natural noise backgrounds. Strengthen predictive models that describe how signal structure and noise environments interact to constrain auditory performance, and develop weighting functions that can be used for species-typical acoustic risk assessments.

APPROACH

Psychoacoustic measurements of hearing are obtained from California sea lions, harbor seals, and northern elephant seals under highly controlled laboratory conditions. Long-term captive subjects are trained using operant conditioning procedures to report the presence or absence of auditory signals in noisy or quiet backgrounds. Testing takes place both under water (in a mapped, reverberant acoustic field) and in air (in a sound-attenuating hemi-anechoic chamber) because the sensitivity and frequency range of hearing in pinnipeds varies significantly as a function of medium. The stimuli presented during testing comprise synthetic and natural sounds that are systematically varied in spectral complexity, or in referential meaning established through explicit associative learning paradigms. The general approach is to obtain absolute detection thresholds for specific complex sounds and compare these thresholds to those previously obtained for pure-tone signals. The tasks are then repeated against a variety of synthetic and natural background masking stimuli to determine the signal-to-noise ratios

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that limit auditory detection, and in some cases, auditory recognition. The methods are modeled in part from studies of bird communication in noise (Dooling et al., 2009; Lohr et al., 2003) and build upon previous research in our laboratory on hearing capabilities and cognitive processing of auditory-visual information.

In addition to using psychoacoustic methods to assess auditory thresholds under varying signal and noise conditions, the metric of reaction time as a proxy for perceptual loudness measurements is investigated by measuring response latency while varying both signal frequency and signal level in acoustic detection tasks. The resultant latency-intensity functions are used to develop frequency-dependent equal latency contours. Equal latency countours should approximate equal loudness countours across the frequency range of hearing (Moody, 1970), and thus may be used to inform the development of accurate auditory weighting functions for pinnipeds.

Field measurements of representative species-typical vocalizations and associated ambient noise are made at pinniped breeding rookeries, and simple propagation models of natural signals through representative environments are generated. The data collected include physical measurements of environmental noise (maximum and equivalent continuous sound pressure level over different time scales) and vocalization parameters (source level, spectral composition, call duration, intercall interval). These data are combined with information about individuals (age, sex, identity, size, reproductive state, dominance status, and spatial movements) so that functional communication can be assessed through field experiments. Collectively, the complementary laboratory and field studies allow effective detection and recognition ranges for biologically relevant sounds to be modeled under various conditions of natural and anthropogenic noise.

Key personnel on the project in FY2012 included the PI, research technician Asila Ghoul, UC Santa Cruz graduate students Jillian Vitacco and Kane Cunningham (Ocean Sciences) and Peter Cook (Psychology), and animal technicians Caroline Casey and Jenna Lofstrom. The field data were collected by the PI, Caroline Casey, and Selene Fregosi with collaboration on field experiments from Nicolas Mathevon from the Universite de Saint-Etienne (Laboratory of Neuroethology) and Isabelle Charrier from the Université Paris Sud (Center for Neurosciences). The entire research program was supported by a team of 19 undergraduate and post-graduate volunteers and interns who received formal training in marine mammalogy and bioacoustic research in exchange for their apprenticeship in the program at the University of California Santa Cruz.

WORK COMPLETED

Just prior to the start of FY2012, the PI suffered a medical trauma that resulted in some delays to the project. An additional complicating factor was the late release of FY2012 funds in spring 2012. As a result, a no-cost time extension was granted to provide twelve additional months to complete the research project. Therefore, a portion of the FY2012 objectives are scheduled to be completed in FY2013.

During FY2012, accomplishments included progress in areas concerning (1) auditory temporal processing, (2) noise-induced persistent threshold shift, (3) use of reactions times as a proxy for auditory weighting functions, (4) detection of complex signals in noise, and (4) field studies of communication in natural noise. Laboratory studies of hearing were conducted with California sea lions and a harbor seal at Long Marine Laboratory; the northern elephant seal that was a long-term participant in this research died in November 2011 at the age of 17 from natural causes. Field research was conducted intensively from December 2011 to early March 2012 at two pinniped rookeries on the central coast of California.

(1) Due to the recent publication of a significant study on temporal processing of acoustic signals by seals (Kastelein *et al*., 2010), we completed a project to directly test the hypothesis that seals may show unusually long integration times for low-frequency auditory signals. We tested a harbor seal listening for 200 Hz tones of either 500 ms or 2500 ms in a sound-attenuating acoustic chamber to determine if the differences reported by Kastelein *et al.* (2010) would be observed. To do this, high-resolution behavioral thresholds were obtained from the seal and reaction times were measured and compared for the two test conditions. The same experiment was then replicated in a calibrated underwater sound field to confirm that the temporal summation of low-frequency sound by seals is unaffected by the media in which the auditory system operates. Additionally, an analysis of temporal processing in a California sea lion was completed for a range of frequencies within the range of best hearing sensitivity. Both studies of auditory temporal processing were accepted for publication during FY2012.

(2) A unique case of noise-induced persistent hearing loss was evaluated in a harbor seal four years following an acoustic injury. Hearing sensitivity at 5.8 kHz was repeatedly measured under water to determine whether progressive recovery of the narrow-band hearing loss had occurred. This case provides the only known information on PTS from acoustic exposure in any marine mammal.

(3) An analysis of auditory weighting functions derived from equal latency contours was completed during FY2012. The idea of developing frequency weighting functions for marine mammals has received considerable attention recently because such filters can determine the relevant bandwidth for noise exposure assessments, and they also take differential auditory sensitivity of different species into account when identifying acoustic risks. However, such weighting functions are difficult to determine for nonhumans as they rely on equal loudness relationships that are subjective. Equal auditory reaction times may serve as possible proxy for equal loudness judgments, because similar reaction times for signals predict similar perceptual loudness of those signals. The primary data for this experiment was gathered from one harbor seal and one California sea lion and was reported during FY2011; the analysis of results and possible applications was completed in FY2012 and is summarized later in this report.

(4) Animal training and technical planning was completed for the complex masking experiments to be conducted in FY2013.

(5) Calibrated recordings of acoustic signals and ambient noise conditions were collected in two unique pinniped breeding areas. The first location, Año Nuevo State Reserve, is located approximately 20 miles north of Long Marine Laboratory, and features breeding colonies of northern elephant seals (*Mirounga angustirostris*), Pacific harbor seals (*Phoca vitulina*), and California sea lions (*Zalophus californianus)*, and Steller sea lions (*Eumetopias jubatus*). The second location, Piedras Blancas, is located just north of Cambria, California and is quickly expanding as one of the largest northern elephant seal colonies along the west coast of North America. Field studies of elephant seal communication in natural noise environments were conducted at both sites between the months of December 2011 and March 2012. Repeated recordings of known breeding males engaged in high-stakes, competitive, behavioral interactions were obtained along with coincident measurements of background noise on the rookery. To support these acoustic data sets, observational, GPS, and

photometric data were collected on all the focal males in the study in order to estimate body size, dominance status and patterns of association and site fidelity within the breeding season. The role of acoustic signals in mediating behavioral interactions was investigated using non-invasive playback methods at both breeding sites in to determine the extent to which call features indicate biologically significant information to receivers. As studies of functional communication in marine mammals are relatively rare, this approach allows the examination of the conditions required for call detection relative to recognition, as demonstrated through measurable and predictable behavioral responses.

RESULTS

(1) The data that we obtained on low-frequency temporal processing of tones by a harbor seal do not support the findings of Kastelein *et al*. (2010) which indicate that integration times for harbor seals exceed 3000 ms for 200 Hz tonal signals. This claim is significant as it implies that currently available hearing data for this species (and other pinnipeds) would greatly underestimate the audibility of certain low-frequency sounds. The results from Kastelein *et al.* (2010) predict a difference of 9 dB between thresholds measured for 200 Hz tones with duration of 500 ms or 2500 ms. However, we found no difference in measured hearing thresholds at these durations for a harbor seal tested in air (30 dB vs. 30 dB, with 95% confidence limits of 28.9-31.0 and 28.8-30.6 dB, respectively) or under water (75 dB vs. 74 dB, with 95% confidence limits of 74.0-76.1 and 73.6-75.0).

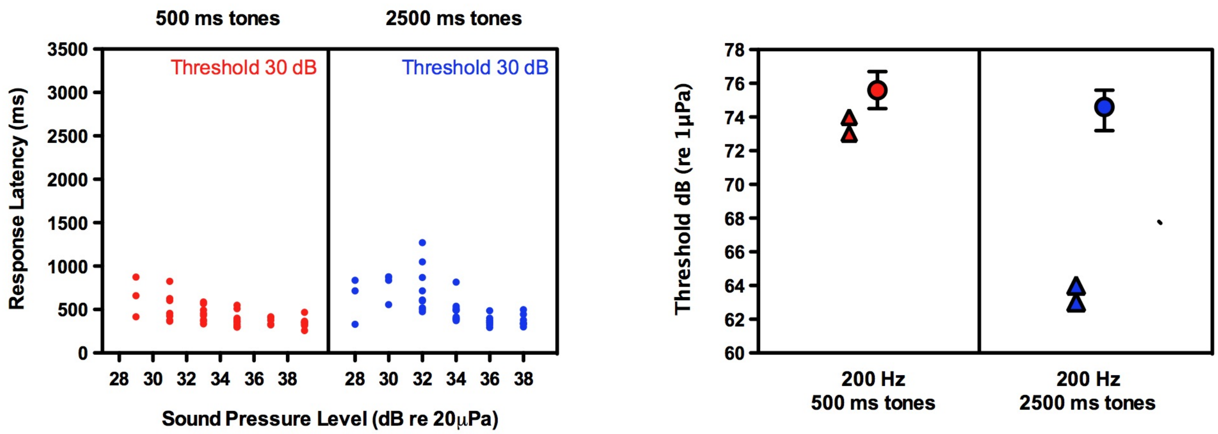

Figure 1. Low-frequency auditory thresholds as a function of signal duration in a harbor seal. (Left panel) Aerial thresholds for 200 Hz signals with durations of 500 ms and 2500 ms were both 30 dB re 20 μPa; corresponding reaction time data show that the excess signal duration did not improve stimulus detection performance. (Right panel) Underwater thresholds for the same 200 Hz signals (circles) are not different for 500 and 2500 ms tones. The data are compared to previously published values (triangles).

(2) The hearing of a harbor seal tested four years following the onset of a small but significant narrow-band hearing loss (centered at 5.8 kHz) showed that hearing sensitivity did not improve with extended recovery time following this event. There was no difference in hearing sensitivity to 5.8 kHz signals when thresholds were compared 180 to 1400 days (4+ years) following the appearance of the hearing loss. A noise-induced persistent threshold shift of 6-7 dB remains evident for this seal, manifested as a ‘notch’ in his aerial and underwater audiograms.

(3) The metric of reaction time proved to be a useful indicator of perceptual loudness for subjects representing two pinniped species. Contours of equal response latency extending across plots of sound pressure level vs. sound frequency showed features similar to that expected from contours of equal loudness. Observed reaction times ranged from 167 to 640 ms in the harbor seal and from 72 to 468 ms in the California sea lion; however, the most informative latency range spanned 200 ms for the harbor seal and 100 ms for the California sea lion across all frequencies tested. This range was bounded at one end by the slowest observed reaction times to the quietest detectable signals and at the other end by the fastest motoric reaction times that could be produced in response to easily detectable (loud) signals. Despite this somewhat limited range of reaction times, the results confirmed that these pinnipeds produced consistent, fast reaction times that provide insight into their perceptual auditory experiences. The informative range of reaction times covered a stimulus amplitude range of approximately 40 dB; that is, a range that extended from the threshold of hearing to ~40 dB above that level.

This dynamic range most closely approximates the A-weighting functions used for measurement of human exposure to environmental and industrial noise, as well as for assessment of potential hearing damage and other noise health effects. However, because human A-weighting is most suitable for low amplitude noise measurements (providing a 40 dB relative equal loudness scale) the utility of this function for marine mammals lies mainly in improving understanding of differential auditory sensitivity as a function of audible sound frequency. Such a function would be less conservative than the currently proposed 'm'-weighting function for marine mammals (see Southall *et al.,* 2007) and is closer to the alternative suggested approach of using the inverted audiogram (i.e., sensation level or hearing threshold sound level) to provide estimated weighting functions for species for which such audiometric information is available.

(4) No new results are available on complex masking at the time of this report; this portion of the study will be completed in FY2013.

(5) A total of 79 individuals were identified and intensively behaviorally and acoustically sampled at the Año Nuevo breeding colony, and 46 individuals were similarly studied at the Piedras Blancas breeding colony during the 2011-12 season. The ritualized calls of reproductively mature northern elephant seals showed several unique characteristics. These calls were highly individually stereotyped. They showed strong individual differences in amplitude, spectral, temporal, and repeatable, complex patterns. These differences were not related to resource holding potential determined by dominance status or body size. The acoustic signatures of individual males were sufficient to encode information about individual identity but did not show strong potential for conveying information about motivational state. Calls were invariant in amplitude within individuals across a variety of escalating behavioral contexts suggesting the absence of the Lombard effect and lack of acoustic scaling with body parameters as have been seen in other marine mammals. Over 500 high quality recordings were analyzed in the 2012 season and 92 field playback experiments were conducted on the basis of the results of this analysis.

Prior correlational analyses had shown that few call features could be reliably linked to the demonstrated resource holding potential of breeding individuals. Playback experiments confirmed that individuals did not respond to acoustic features that were weakly associated with size and status, even as these features were systematically manipulated to optimize information content. Rather, males clearly demonstrated associative learning of caller identity through repeated pairwise behavioral interactions, emphasizing the role of call recognition, experience, and long-term memory in managing high-stakes social behavior with biologically significant acoustic cues.

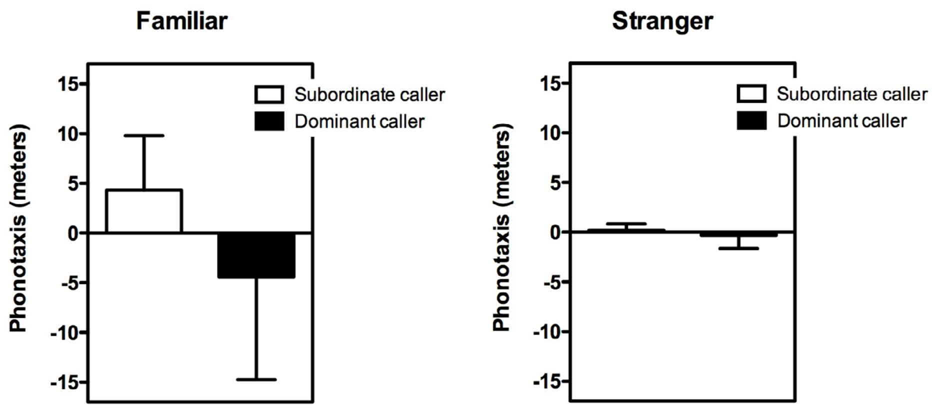

Figure 2. Phonotaxis of focal elephant seals observed during field playback experiments. (Left panel) Breeding males showed significant approach to the speaker when the playback was from a familiar subordinate caller, and significant retreat from the speaker when the playback was from a familiar dominant caller. (Right panel) Breeding males tested at a remote location showed no differential phonotaxis to the calls of unfamiliar breeding males, indicating that the information contained in individually unique calls is associatively learned by males within the breeding colony.

IMPACT/APPLICATIONS

The audiometric data generated by this project and preceding projects have contributed to noise exposure criteria developed specifically for free-ranging marine mammals, which in turn are used by the operational Navy, industry, and U.S. and International regulators to establish appropriate guidelines and mitigation for anthropogenic noise emissions in marine environments. We expect that the results concerning weighting functions derived from reaction times will inform development of frequency selectivity filters used in noise assessment metrics.

RELATED PROJECTS

An Opportunistic Study of Hearing in Sea Otters (Enhydra lutris): Measurement of Auditory Detection Thresholds for Tonal and Industry Sounds. C. Reichmuth (UC Santa Cruz) is the PI; the project is supported by the Bureau of Ocean Energy Management (BOEM). This project expands upon auditory research with pinnipeds by examining hearing in another marine carnivore, the southern sea otter. There is overlap in facilities, experimental resources, and personnel.

Airgun Effects on Arctic Seals: Auditory Detection, Masking, and Temporary Threshold Shift. C. Reichmuth (UC Santa Cruz) is the PI; the project is supported by the Joint Industry Programme on Sound and Marine Life. This project expands upon auditory research with pinnipeds by examining hearing and the effects of noise in arctic seals. There is overlap in facilities, experimental resources, and personnel.

Detection and Tracking of Submerged Hydrodynamic Wakes Using a Bioinspired Hybrid Fluid Motion Sensor Array. B. Calhoun (U Virginia) is the PI, C. Reichmuth (UC Santa Cruz) is co-PI; the project is supported by the Office of Naval Research (N00014-09-10468). Field testing of sensor design is conducted at Long Marine Laboratory with one of the seals involved in the current project. There is overlap in facilities, experimental resources, and personnel.

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